"Patterns of carnivore species co-occurrence in North Rim, Grand Canyon National Park, Arizona"

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Abstract

Successful conservation and management of ecosystems requires an understanding of the mechanisms determining community assembly. Classic laboratory and field experiments have clearly demonstrated the local incidence of negative interspecific interactions such as predation and competition, but interpretation of evidence of competitive structure at the scale of species communities has been controversial. In this pilot study we explicitly quantify patterns of community structure at the landscape scale by examining patterns of species co-occurrence in a single, contiguous terrestrial ecosystem. The Ponderosa Pine forest ecosystem of the North Rim of Grand Canyon National Park is relatively homogeneous and historically unmodified and supports at least ten, extant species of native carnivores. Using a Geographic Information System (GIS) database, we selected twenty sites to randomly sample carnivore species presence across the landscape while minimizing variation in habitat variables, such as elevation and forest cover. Sites were sampled during the summer of 2003 using a suite of passive wildlife monitoring techniques, including hair traps, remotely-triggered cameras, scat and track surveys. A Monte Carlo null model analysis of resulting species detections does not show evidence of significant structure at the community scale, pairs of species show limited coexistence, and coyotes and bobcats co-occur less frequently than would be expected by chance. In addition, the various survey methods had different levels of success in detecting the target species. Transect searches resulted in the greatest proportion (73%) of detections, while camera traps were most effective for detecting coyotes and some infrequently detected species (gray fox and spotted skunk), and hair traps were generally ineffective. Quantifying co-occurrence patterns in the North Rim ecosystem will provide a baseline for assessing future trends in carnivore populations and distributions in Grand Canyon National Park and contribute to methods for predicting species distributions and habitat suitability in more complex, modified ecosystems.

Keywords

Grand Canyon National Park, mesocarnivore, null model analysis, community structure, co-occurrence, competitive exclusion

Introduction

Extinctions of mammal species in U.S. national parks (Newmark 1995; Parks & Harcourt 2002) have led to increased concern about the fate of species, especially carnivores, remaining in the reserve system. Carnivores often function as keystone species (Power et al. 1996), affecting trophic patterns and processes directly through predation (sea otter example) and indirectly through scavenger subsidies (Wilmers et al. 2003), and their removal and reintroduction can have dramatic effects on community structure and stability (bass example). Wide-ranging and low-density species such as carnivores are particularly at risk due to effects of reserve size and isolation, and are most exposed to edge effects and external threats posed by humans (Woodroffe & Ginsberg 1998).

Regional planning efforts and large-scale viability assessments require reliable baseline monitoring data in order to detect trends in species distribution and abundance. Carnivore species, with the exception of mountain lions, have never been comprehensively surveyed in Grand Canyon National Park (U.S. National Park Service). Spatial patterns of coexistence among species may be important toward estimating broad scale species distributions and habitat suitability, and community scale surveys can be limited by sample effort and extent and often require the use of opportunistic or remote measures.

The local incidence of such negative interspecific interactions as predation and competition has been demonstrated in classic laboratory and field experiments (Huffaker 1958; Connell 1961), but their impact has been difficult to quantify at community scale and is generally neglected in standard survey and monitoring approaches. Research on spatial use patterns among sympatric carnivores is generally based on relatively small numbers of radio-collared species (Riley et al. 2003) or individual animals (Fedriani et al. 1999; Fedriani et al. 2000; Neale & Sacks 2001a; Neale & Sacks 2001b; Iberian Lynx paper). However, local distributional relationships among species could be critical in designing sampling schemes and making regional-scale population estimates.

Null model approaches present an opportunity for quantifying community structure among carnivore species at greater scales. Simberloff and Connor (1979) proposed to assess community assembly by using a null-model approach to look across datasets for multiple systems to determine whether patterns of species co-occurrence are non-random. Reevaluating Diamond's (1975) bird distribution data, they rejected the hypothesis of competitive structure, attributing patterns in species composition to chance colonization events. However, many concerns associated with Monte Carlo randomization approaches and indices of community structure have been addressed (Gotelli 2000), and a recent meta-analysis of 96 data sets encompassing a variety of taxa and ecosystems shows that patterns of species co-occurrence are highly non-random according to several well-tested indices of community structure (Gotelli & McCabe 2002). Meta-analysis approaches, while important to the development of a general theory of community structure, are

limited by inconsistency in methods of data collection and analysis, variation among taxa and ecosystems, and in their capacity to characterize particular systems. Therefore, this study proposes to test local mechanisms of community assembly by examining patterns of species co-occurrence among carnivore species in a single, contiguous terrestrial ecosystem.

This study is a preliminary approach toward developing a sampling framework for measuring the effects of species co-occurrence patterns on the distribution and viability of the carnivore community in Grand Canyon National Park. The relative homogeneity of the Ponderosa Pine forest of the North Rim region of the park allows isolation of spatial patterns of coexistence among species by controlling for habitat variation among sites. However, it should be noted that the number of sites is relatively low (n=20), the species are low-density and elusive, and sample effort was limited to one season. It is our hope that the results of this research will establish a baseline dataset for additional research on both target and non-target species as well as a basis for comparison of the effectiveness of various passive wildlife monitoring techniques. The study introduces a relatively simple methodology for tests of carnivore community structure that can be generalized for comparison across trophic levels and among sites, and could serve as a pilot for longer-term (multiple season) monitoring or larger (regional or continental) scale analyses. Finally, understanding co-occurrence patterns at a landscape scale in unfragmented habitat may prove important to assessing species distributions and habitat suitability in more complex, modified ecosystems and informing relevant conservation and management applications.

Methods

Field Methods

Research was conducted in the North Rim region of Grand Canyon National Park, Arizona, U.S.A. This region of the park is located on the Kaibab plateau, a sky island [geologic history] characterized by dominant Ponderosa Pine and mixed conifer forest communities.

Twenty sites were randomly selected to sample carnivore species presence across the study area (Fig. 1). A geographic information system (GIS) database developed by Grand Canyon National Park was used to select sites that were in primary Ponderosa Pine forest, and to minimize variation in elevation and topography. Sites were located a minimum of 4km apart, in order to ensure independence among sites with respect to individual dispersal distances, while maximizing the number of sites that could be monitored in the region. Sites were oriented North-South and 4 ha (200m x 200m) in area. This sampling grain was selected to be within the order of magnitude of the home range territory of the smallest species surveyed (Zielinski et al. 1995) while a manageable scale for monitoring by one to two field technicians. Sites were established and monitored three times during the summer season between June – August, 2003. Monitoring intervals were 14-21 days, with sites established for a total of 28 – 37 days each.

A suite of three passive wildlife monitoring methods was used to maximize the likelihood of detecting all target species. During each site visit, observer(s) walked four 200m N-S transects through the site to record scat, tracks, burrows, and other sign. Scats, tracks and burrows were measured and photographed, and scat samples were collected for future analysis. Scats, tracks, and burrows were identified in the field by size, shape, context and content (Murie 1975; Halfpenny 1986).

A single N-S transect of five hair trap stations, spaced 100m apart, was established through the center of each site. This portion of the research complements an ongoing survey of mountain lion population structure, kinship, movement and habitat use on both rims of Grand Canyon National Park. Hair trap stations included an elevated visual attractant and a padded hair snag (Silver Cloud Associates, LLP, Libby, Montana), each baited with a scented lure (1:1:8 ratio of propoylene glycol, glycerine and beaver castorium with several drops of catnip oil and puma or bobcat urine). Hair trap stations were checked for hair, rebaited and replaced if necessary during each site visit.

A single remotely-triggered camera was placed at the center of the site and baited with a pork short rib. Several different brands of cameras were used (DeerCam, WildifePro, and VanCam; add mfrs.), and to minimize variation in performance, set to night-only mode and trigger intervals of 1.5 – 3 minutes when possible. Camera performance was assessed and film was collected at each site visit, and target locations were re-baited if necessary.

Tree density, slope, aspect, and prey species sign were recorded for each site. In addition, scat, tracks, and other sign were recorded opportunistically during hikes to site visits. The same protocol for recording and collecting sign was followed as in the site protocols.

Analysis

Field identifications of species detections were confirmed according to size and morphology using photo records and scat samples (Murie 1975; Halfpenny 1986), and a subset of scat sample identifications were repeated by a scent discrimination dog (Smith et al. 2003; Reed, unpub. data). Signs that were too old or unclear for species identification were not considered in the analysis. In many cases individual species were detected more than once in a single site, but given the relatively small site scale and low sample effort, the analysis was limited to species presence. Confirmed species occurrences were organized in a presence-absence matrix and analyzed using Monte Carlo null model randomization methods for patterns of community structure and species co-occurrence.

The statistical software package EcoSim (Gotelli & Entsminger 2001) was used to generate random simulations of community distribution patterns and to quantify indices of community structure. We ran 10,000 simulations using an algorithm that distributed the observed number of occurrences for each of the six species with equal probability

among the 20 sites; this algorithm was selected with the assumption that both habitat quality and sample effort were homogeneous among sites. We then compared the observed pattern of community structure to the randomly generated distribution using the checkerboard (C-score) index (Stone & Roberts 1990), which quantifies the average number of checkerboards (sites in which two species fail to co-occur) of all species pairs. The C-score index of community structure was selected for this analysis because it measures patterns of interspecific exclusion without being overly sensitive to noise in the data and has good statistical properties (low type II error rate) when paired with an equiprobable randomization algorithm (Gotelli 2000).

Microsoft Excel was used to generate random simulations of distributional relationships between individual pairs of species and to quantify indices of co-occurrence. This analysis was limited to species with greater than two detections, yielding a total of six possible pairwise comparisons. For each pairwise comparison, we ran 10,000 simulations that distributed the observed number of occurrences for each species with equal probability among the 20 sites. We then compared the observed pattern of species co-occurrence to the randomly generated distribution using the standard score (Z-score) index (Zar 1996), which quantifies the probability of observing a value less than or equal to the actual rate of co-occurrence given the randomly generated null distribution.

Finally, detection rates were summarized by species and monitoring method, in order to identify the most efficient methods for future sampling efforts.

Results

Six extant species of native carnivores were positively detected in one or more sites, including mountain lion (*Puma concolor*), coyote (*Canis latrans*), grey fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), and spotted skunk (*Spilogale gracilis*). Detection results are summarized in a presence-absence matrix (Table 1). We also found possible sign of two additional species, striped skunk (*Mephitis mephitis*) and long-tailed weasel (*Mustela frenata*). Several carnivore species historically present in North Rim, including grey wolf, black bear, raccoon, and ringtail, were not detected.

Using the checkerboard score index of community structure, in a competitively structured community one would expect that the C-score for the observed community would be significantly greater than the expected value generated by null model simulations. We found the C-score of the observed community was not significantly different (P=0.38) than expected by chance.

Using the Z-score index of species co-occurrence, among pairs of species with exclusive distributions, the observed rate of co-occurrence would be significantly less than the expected value generated by null model simulations. We found that three species pairs had rates of co-occurrence less than that expected by their background detection rates (Table 2), and the rate of co-occurrence between bobcats and coyotes was significantly less than that expected by chance (P<0.05; Fig. 2).

The three primary survey methods – hair traps, camera traps, and transect searches – had different levels of success in detecting the carnivore species present in the North Rim sites. Transect searches were the most effective for detecting the carnivore community as a whole, documenting a total of 30 occurrences of five species and the only confirmed detections of mountain lions and bobcats (Table 3). The camera traps were particularly effective for documenting coyotes in sites in which they were otherwise undetected, and resulted in the only confirmed detection of a spotted skunk (Fig. 3). The hair traps were relatively ineffective, resulting in only one hair sample that was visually identified as canid pending genetic analysis.

Discussion

In the course of monitoring the 20 North Rim sites, we failed to confirm detection of several species that are not currently known to be extirpated from any region of Grand Canyon National Park, including black bear, raccoon, ringtail, long-tailed weasel and striped skunk. While survey effort was not sufficiently intensive to determine the true absences of species not detected, further research regarding the fate of these species is warranted. Inventory data would benefit local management and restoration activities as well as assessments of the conservation effectiveness of U.S. protected areas, which are limited by inconsistent records among parks (Parks & Harcourt 2002).

We were unsurprised that we failed to detect significant structure at the community scale. The null model methods of analysis were designed for investigation of patterns at larger scales than the set of North Rim sites (Gotelli & McCabe 2002), among interacting populations of species rather than local distributions of interacting individuals. It would be more appropriate to assess community assembly patterns between the North Rim of Grand Canyon and other natural habitat islands (plateaus) or man-made islands (protected areas) when reliable inventory data are available.

In conducting the pairwise species analyses, we did find significant evidence of limited co-occurrence patterns between coyotes and bobcats, and trends indicating possible spatial interactions between coyotes and foxes and coyotes and badgers. Prior research has shown that carnivore species respond differently to variation in habitat quality and configuration (Fedriani et al. 2000; Virgos et al. 2002; Riley et al. 2003; Hilty & Merenlender 2004). Our results indicate that in the homogeneous habitat type of the North Rim, interspecific effects may structure local species distributions. These results are concurrent with limited home range and territory overlaps among bobcats, coyotes and gray foxes that have been detected by other researchers (Fedriani et al. 1999; Fedriani et al. 2000; Neale & Sacks 2001a; Neale & Sacks 2001b). For example, Neale & Sacks (2001b) found that in undeveloped habitats an average of 16% of a bobcat's home range overlapped neighboring coyote home ranges. Given the limited scale of the monitoring sites (4 ha) relative to the range of bobcat home range sizes in the literature (24 – 563 ha; Crooks 2002), it is reasonable to expect that species with segregated territories would rarely be detected in the same sites. However, it is important to note that the significance levels of these results are highly sensitivity to false absences. If one

more bobcat were detected in a site where a coyote occurred, the difference between the expected and observed rates of co-occurrence would no longer be significant (P=0.32). Similarly, if one more fox or badger were observed in a site where a coyote did not occur, the trends indicated by those results would become significant (P<0.05). In order to better assess the importance of carnivore co-occurrence patterns, sample effort should be directed at a greater number of sites in the North Rim and other ecosystems.

In general, models of habitat suitability and probability of occurrence for multiple species are exclusively based on site and landscape variables related to habitat quality (e.g., Virgos et al. 2002). Other researchers have shown the distribution and abundance of predators, especially coyotes, are important determinant of the composition of the rest of the community (Crooks & Soule 1999) and in some cases could be the most important explanatory variable for predictive models of species occurrence (Hilty). Excluding interactive species from models could result in overestimation of population size, density and probability of occurrence. Our results suggest that short of a full, community-scale inventory, rates of co-occurrence among territorial species should be estimated and incorporated into predictive models.

An improved understanding of co-occurrence patterns among carnivore species is beneficial for modeling species distributions within the protected area of Grand Canyon National Park, but there may also be important consequences for fragmented and modified systems. For example, habitat fragmentation and modification limit spatial use by bobcats and coyotes (Riley et al. 2003), and we may see differential responses to landscape change across the carnivore community. In addition, invasive species can alter community structure (Sanders et al. 2003) and the expansion of invasive (domestic cat) and human commensal (raccoon) predators in developed areas of the park (T. Holigay, pers. com.) may pose significant threats. Understanding these distributional patterns in the absence of invasion may be useful for assessing its effects.

The three primary passive wildlife monitoring methods employed in our research had variable success in detecting the different carnivore species occurring in the North Rim sites. Taken together, results from the camera traps and transect searches were adequate to capture the full complement of carnivore species detected. Transect searches provided the majority (73%) of the data, while photographs provided unequivocal species identifications and detections of rarer species. For example, camera trapping resulted in the only detection of a spotted skunk on the North Rim since a museum sample was collected in 1963 (C. Hyde, pers. com.). Hair trapping, by contrast, was relatively ineffective, yielding only one sample of unclear origin. Track plates were untested in this system, but prior research has shown them to be less effective at detecting carnivore species even when unbaited (Hilty & Merenlender 2000).

For the purposes of future research, we recommend increasing transect search effort per site, and pairing transect searches with baited remotely-triggered cameras. It is unclear how much bias was introduced by baiting the camera stations, in that the scent may have attracted individuals that would not have otherwise occurred in the sites. However, we felt it was necessary given a random design in a homogeneous study area, and sought to

minimize its effects by placing the cameras at the centers of the sites. Furthermore, given the very low detection rate of the hair trap effort, it seems unlikely that the scent lure on the hair traps contributed to attracting individuals into the sites. We feel that hair traps are ineffective for broad community surveys, but they may be useful for generating critical data for in-depth population and genetic studies of particular species.

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Tables

Table 1

	Site																			
Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
Mountain lion	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Coyote	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	1	1	0	0
Fox	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1
Bobcat	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Badger	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1
Spotted skunk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 2

Species pair	*Expected ($\mu \pm$ s.d.)*	*Observed*	*Z-score*	*P*
Coyote / Bobcat	0.14 + 0.05	0.05	1.67	< 0.05
Coyote / Fox	0.06 + 0.04	0	1.52	0.06
Coyote / Badger	0.12 + 0.05	0.05	1.38	0.08

Table 3

			Transect search		
Species	*Hair*	*Photo*	Scat	Track	Burrow
Mountain lion	0	0	3	0	0
Coyote	*	7	4	2	0
Fox	*	1	2	0	0
Bobcat	0	0	9	2	0
Badger	0	1	0	0	8
Spotted skunk	0	1	0	0	0
Total	1	10	18	4	8

Figures

Fig. 1

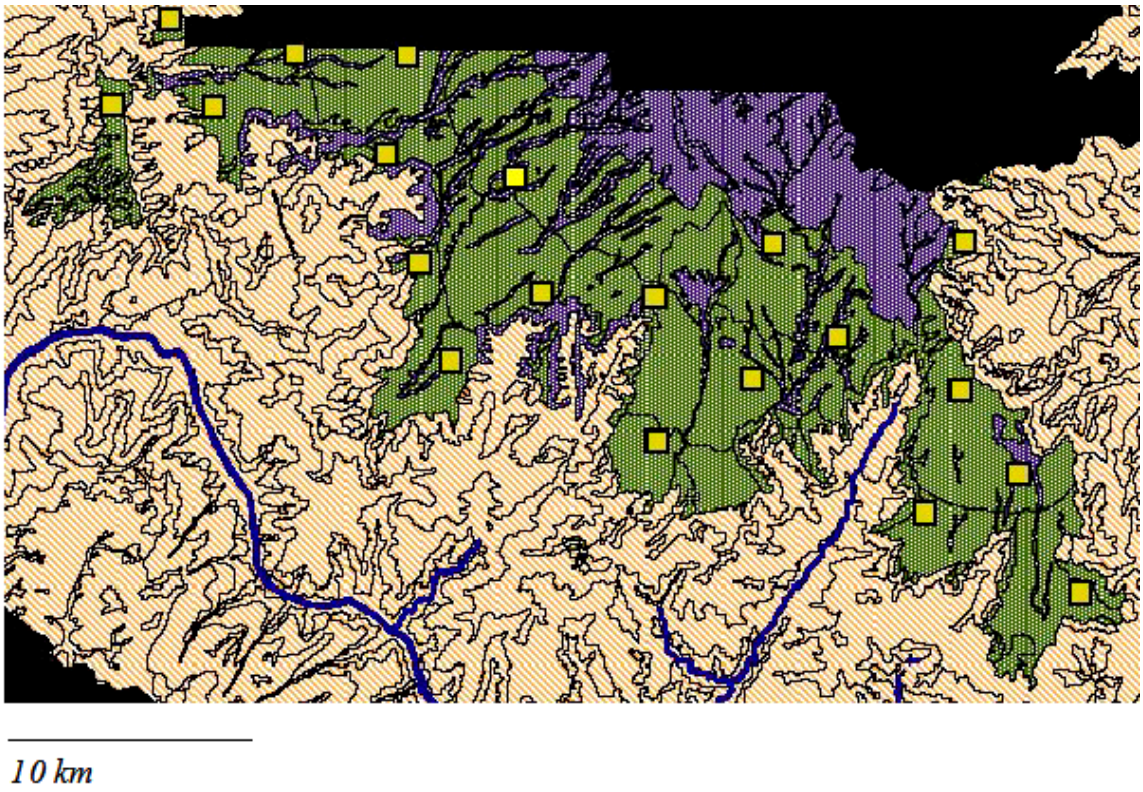
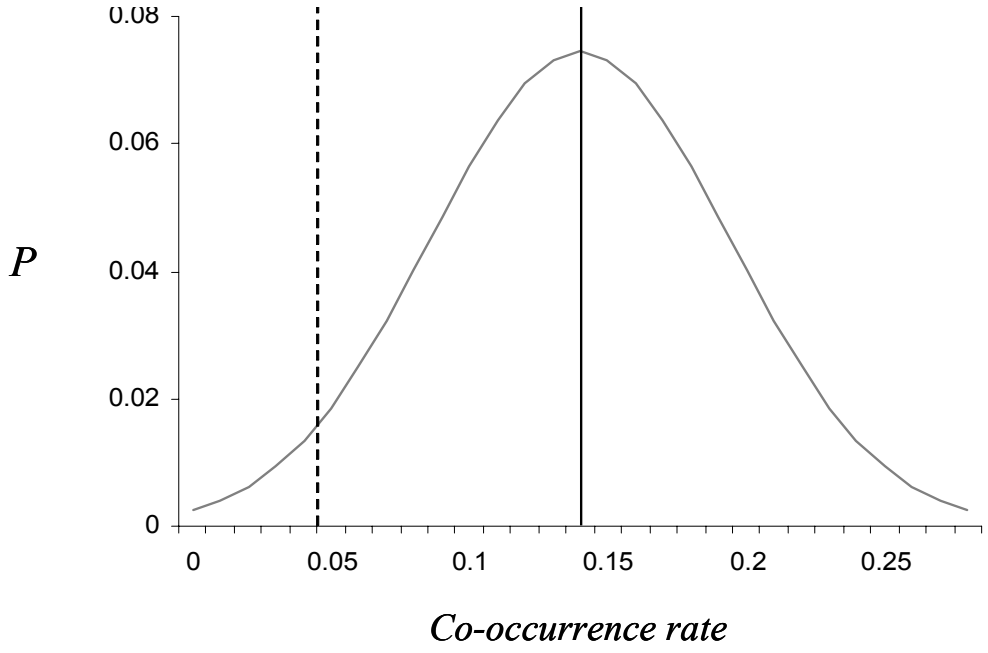
Fig. 2